Growth and Production in Exploited and Unexploited Populations of a Rocky Shore Gastropod, *Turbo sarmaticus*

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(10 Text figures)

INTRODUCTION

THE "ALIKREUKEL," *Turbo sarmaticus* Linnaeus, 1758 is a large edible gastropod, common on rocky shores along the south coast of South Africa where it is collected privately for eating and for use as bait. Unlike the "perlemoen," *Haliotis midae,* it is not exploited commercially despite the large populations that may develop in the lower intertidal and subtidal zones. The only completed work on this species is a paper on biochemical composition (McLACHLAN & LOMBARD, 1979) and an unpublished M. Sc. thesis by Lombard in 1977. Growth has been studied in some other intertidal gastropods from rocky shores in this region (NEWMAN, 1968; BRANCH, 1974), but no production estimates have been published.

The aims of this study were to obtain information on growth and production in *Turbo sarmaticus* near the centre of its range. The close proximity of both an exploited population and a population subject only to natural mortality allowed further investigation of the effects of removal of adults on population structure and production in a large edible gastropod.

MATERIALS AND METHODS

Two study areas were chosen on opposite sides of the headland at Cape Receife near Port Elizabeth, 34°00′S, 25°30′E. Flat Rocks faces north eastwards and is partly protected from the swell (which approaches mainly from the south-west) by the headland. The second area, Skoenmakerskop, faces southwards and is exposed to fairly heavy wave action. Flat Rocks is a boulder strewn shore of gentle slope while Skoenmakerskop is steeper with deep pools and gullies. Temperatures in the shallows at Port Elizabeth have an annual range of 10-25°C with monthly means of about 21°C in January and 15°C in July and August. Temperatures at Skoenmakerskop can occasionally be several degrees lower than at Flat Rocks due to brief local upwelling in summer. The *Turbo sarmaticus* population is heavily exploited at Flat Rocks but virtually untouched at Skoenmakerskop because of its limited accessibility.

Morphometric Characteristics

To obtain the relationship between shell breadth, shell "length" and operculum diameter 70 animals collected from both localities and covering a full size range were measured to 0.1 mm with vernier calipers. These measurments are illustrated in Figure 1. Shell breadth/dry body mass relationships were determined for 61 animals from Skoenmakerskop and 88 from Flat Rocks. Shell breadth was measured to 0.1 mm and dry mass obtained at 100°C after removal of shell and operculum.

Sampling

Because of a vertical zonation of size classes, sampling covered the whole zone occupied by *Turbo sarmaticus* down to about 1 m below the spring low tide level (LWS). The intertidal area over which animals were collected totalled 460 m² at Skoenmakerskop and 600 m² at Flat Rocks. Sampling was done every second month from February 1975 to July 1976. All animals were measured to

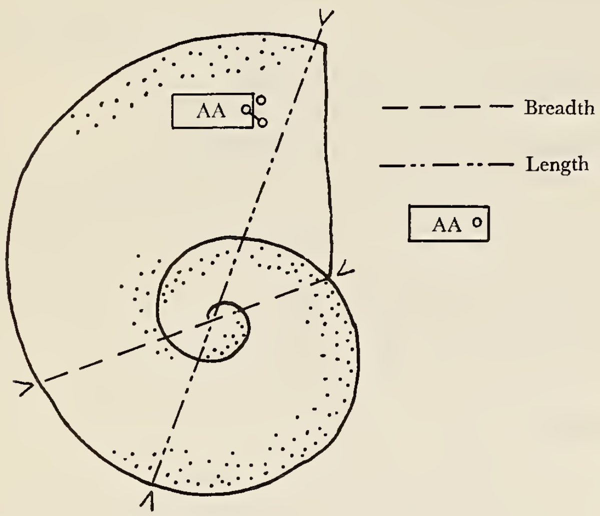

Figure 1

View of *Turbo sarmaticus* from above the spire showing length and breadth measurements and position of plastic tag

1 mm shell breadth and immediately returned to the collection area.

Growth Estimate

From the sampling results length/frequency histograms with 4 mm class intervals were constructed and year classes separated using probability paper (Cassie, 1954).

Tagging was also used to estimate growth rates. At Skoenmakerskop 187 animals larger than 20 mm shell breadth were tagged in May 1975. This was done by taking them back to the laboratory, drilling 2 small holes above the aperture (Figure 1) and attaching a small plastic tag with nylon line. All animals were measured to 0.1 mm shell breadth and returned to the collection area within 24 hours after being kept overnight in an aquarium. This was not done at Flat Rocks because of human interference.

From both the mean values from the size/frequency histograms and the tagging results Ford-Walford plots were constructed to estimate the constants L_∞ and K in the von Bertalanffy growth equation (Crisp, 1971) which is:

$$L_t = L_\infty (1 - e^{-K(t-t_0)})$$

where L is shell breadth at age t, L_∞ is the average maximum shell breadth to which animals in the sampled population grow, K is a constant ($\frac{1}{3}$ of the rate of katabolism) and t_0 is the hypothetical age when *Turbo sarmaticus* would have had a shell breadth of 0 mm if it had grown according to the equation.

Growth rings could not be identified in the opercula.

Production

Production was estimated for each age class as both growth and mortality at both study areas as outlined by Crisp (1971):

$$P_G = \Sigma_t \Delta\overline{W}_t \cdot \overline{N}_t$$

where P_G is production by growth, $\Delta\overline{W}_t$ is the increase in mean individual mass over time interval t and $\overline{N}_t$ is the mean number of individuals in the year class over time interval t.

$$P_M = \Sigma_t \Delta\overline{N}_t \cdot \overline{W}_t$$

where P_M is production by mortality, $\Delta\overline{N}_t$ is the decrease in numbers over time interval t and $\overline{W}_t$ is the mean individual mass over time interval t.

RESULTS

Morphometric Characteristics

The relationships determined were as follows:

Operculum diameter (mm) = 0.504 shell breadth (mm) + 1.791 ($r = 0.997$, $p < 0.001$)

Shell length (mm) = 1.232 shell breadth (mm) + 2.751 ($r = 0.999$, $p < 0.001$)

For Flat Rocks:

Log dry mass (mg) = 2.36 $\log_{10}$ shell breadth (mm) − 0.207 ($r = 0.993$, $p < 0.001$)

For Skoenmakerskop:

Log dry mass (mg) = 2.89 $\log_{10}$ shell breadth (mm) − 0.173 ($r = 0.989$, $p < 0.001$)

Skoenmakerskop animals are initially heavier but by a shell breadth of about 70 mm have become lighter than animals of the same shell breadth at Flat Rocks. The latter 2 regressions did, however, not differ significantly (analysis of covariance) and are illustrated in Figure 2.

Population Sampling

On both shores the populations exhibited vertical size class zonation with small individuals in rock pools on the mid shore and large animals at and below LWS (Figure 3), this trend being significant (linear regression, $p < 0.05$) on both shores. The size/frequency histograms for Skoenmakerskop and Flat Rocks are given in Figures 4 and 5 with 4 mm shell breadth intervals. The mean

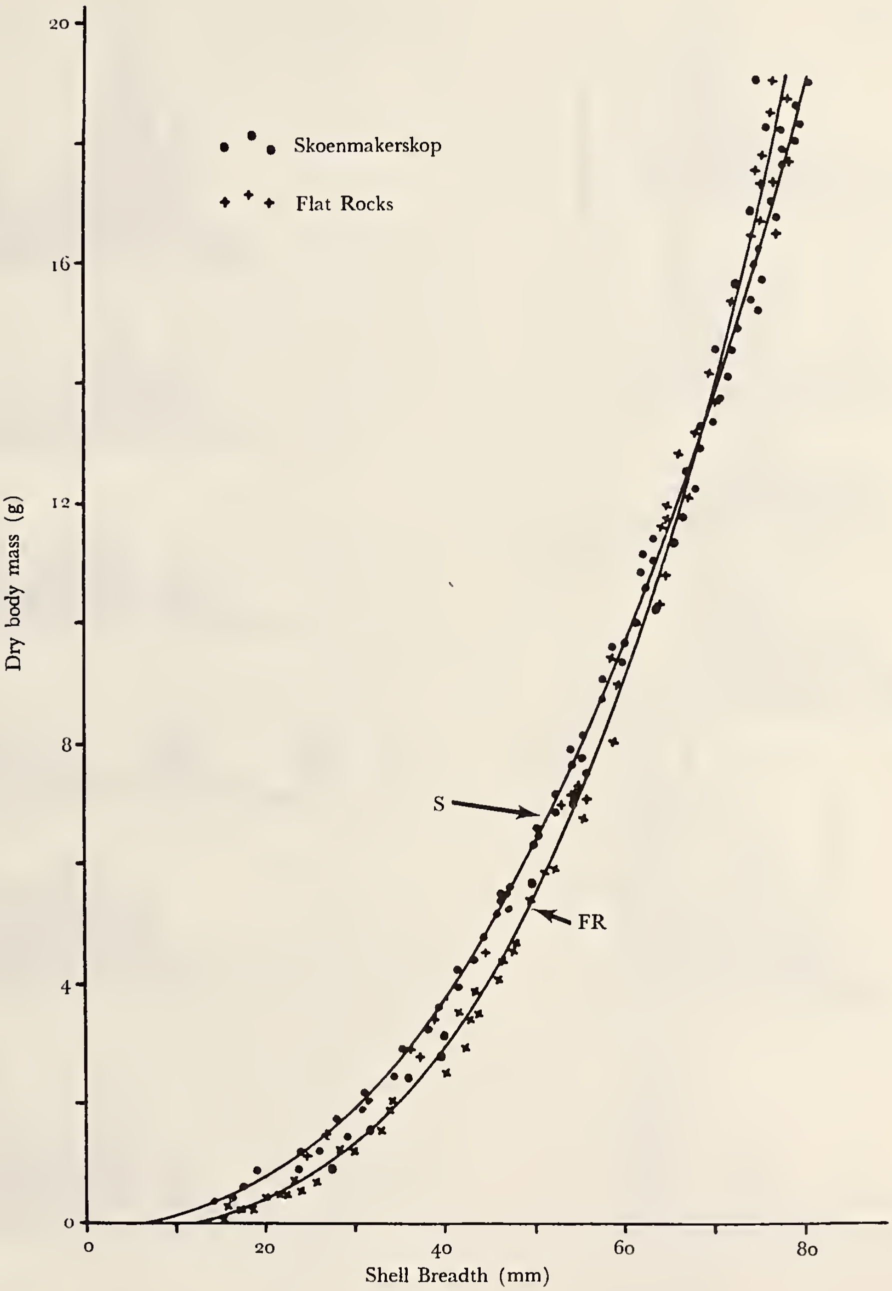

Figure 2

The relationship between dry body mass and shell breadth for *Turbo sarmaticus* from Skoenmakerskop and Flat Rocks. See text for equations

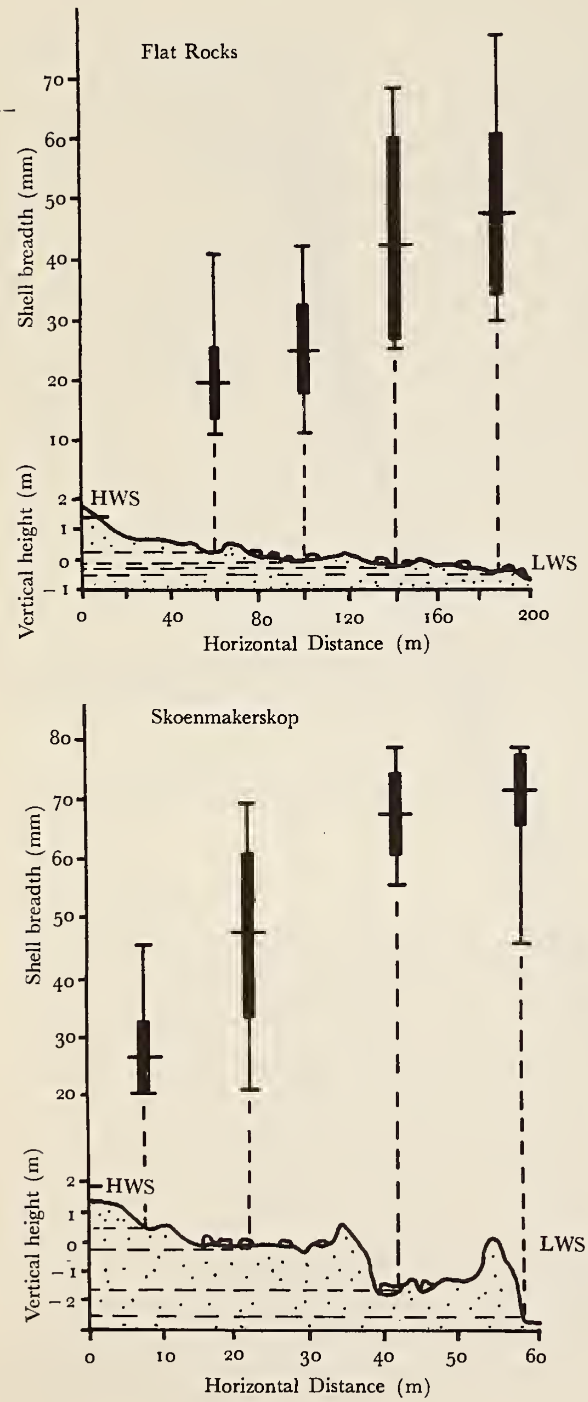

Figure 3

Profiles of the intertidal zones and intertidal size distributions of *Turbo sarmaticus* at Flat Rocks (above) and Skoenmakerskop (below). Vertical heights are from mean low water of springs. Means ± one standard deviation and ranges of size of *Turbo sarmaticus* are indicated

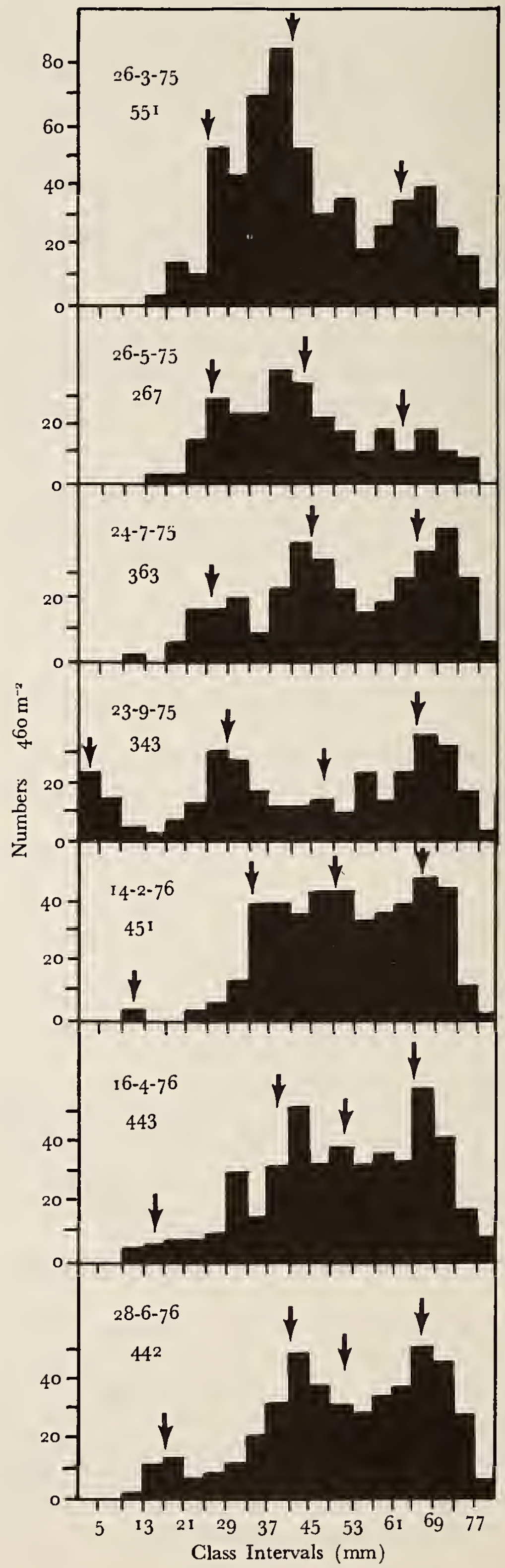

Figure 4

Figure 5

Size frequency histograms for *Turbo sarmaticus* from Flat Rocks. Dates of sampling and total number of animals collected are indicated. Arrows indicate cohort means

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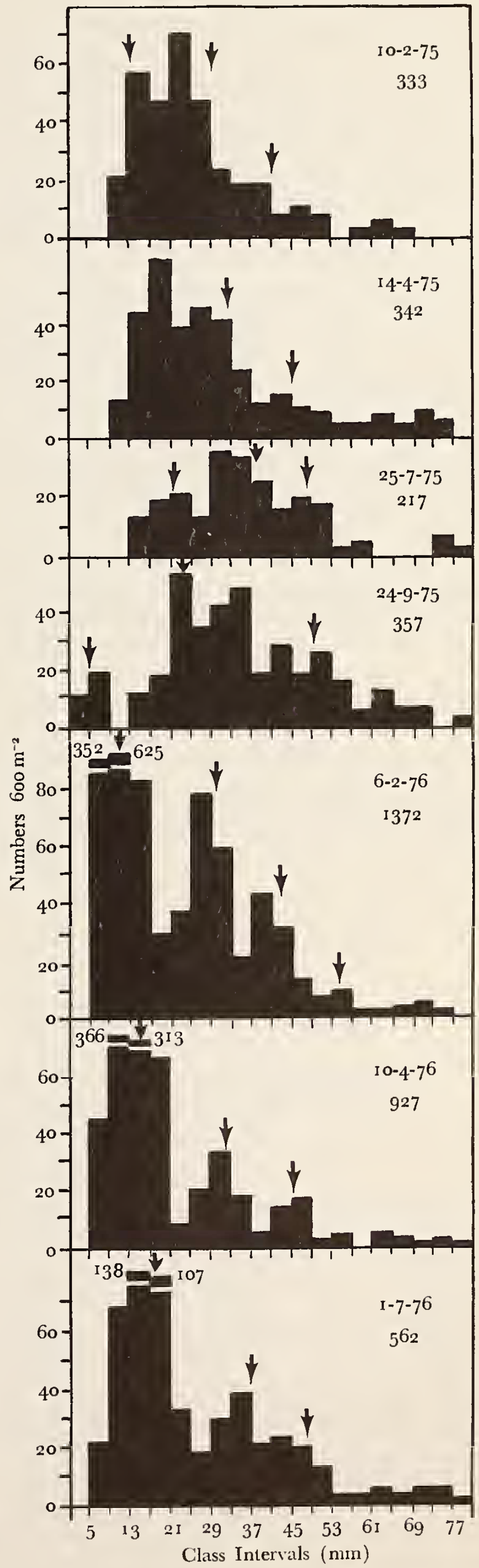

values for shell breadth for year classes separable with probability paper are indicated with arrows. Three classes were separable at Skoenmakerskop and 4 at Flat Rocks. The smallest class was first collected in September with mean shell breadth around 5 mm at both areas. Spawning occurs during November-March (LOMBARD, 1977) and settlement was therefore probably mainly in July.

Tagging

Forty-eight tagged animals were recovered of which 8 were recovered twice and one 3 times. Figure 6 illustrates growth rates of animals in the size classes 21-40 mm, 41-60 mm and > 61 mm shell breadth based on growth increments between tagging and recovery. Faster growth rates for the smaller classes and increased growth in summer are clearly evident. In Figure 7 this is converted to depict growth increments as a function of initial shell breadth, and mean values from the size/frequency histograms are included.

Growth

The Ford-Walford plot with the histogram and tagging data is given in Figure 8. The 3 lines shown do not differ significantly (analysis of covariance). As the tagging data cover mainly the larger sizes and mean values from the histograms cover the smaller sizes, the two were pooled for Skoenmakerskop to obtain a combined equation:

$$L_{t+1} = 0.644 l_t + 28.505 \; (r = 0.989, \; p < 0.01)$$

From these data L_∞ and K in the von Bertalanffy growth equation are 80.070 and 0.440 for Skoenmakerskop and 86.857 and 0.271 for Flat Rocks. The following

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Figure 4

Size frequency histograms for *Turbo sarmaticus* from Skoenmakerskop. Dates of sampling and total number of animals collected are indicated. Arrows indicate cohort means

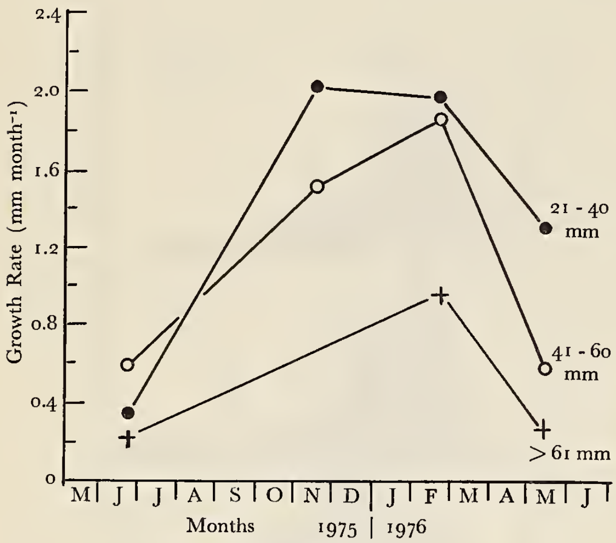
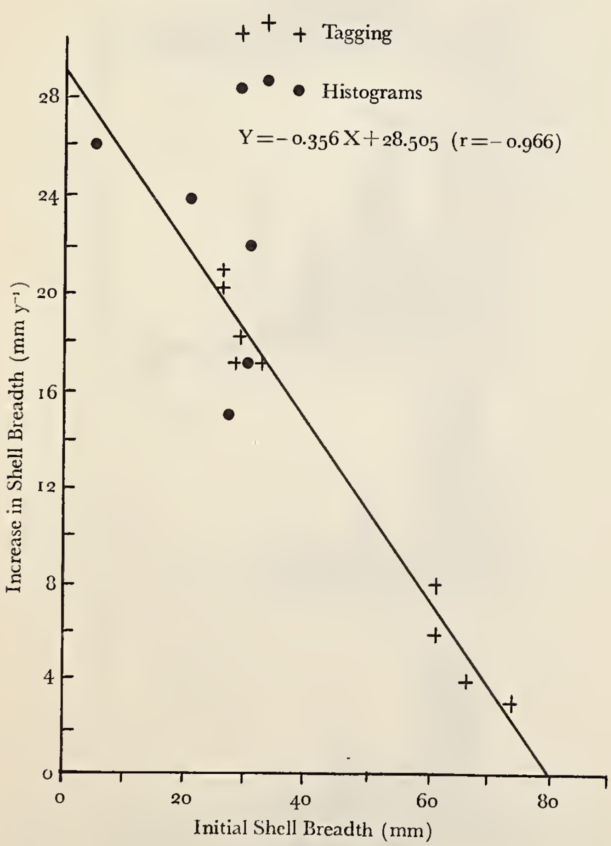


Figure 6

Growth rate of three size classes (given in mm shell breadth) of *Turbo sarmaticus* at Skoenmakerskop based on tagging results



von Bertalanffy growth equations are then derived for these 2 populations (Figure 9):

Skoenmakerskop: $L_t = 80.07(1 - e^{-0.44(t+0.0227)})$

Flat Rocks: $L_t = 86.857(1 - e^{-0.271(t+0.138)})$

This suggests that growth is initially faster at Skoenmakerskop but levels off sooner at Flat Rocks (Figure 9).

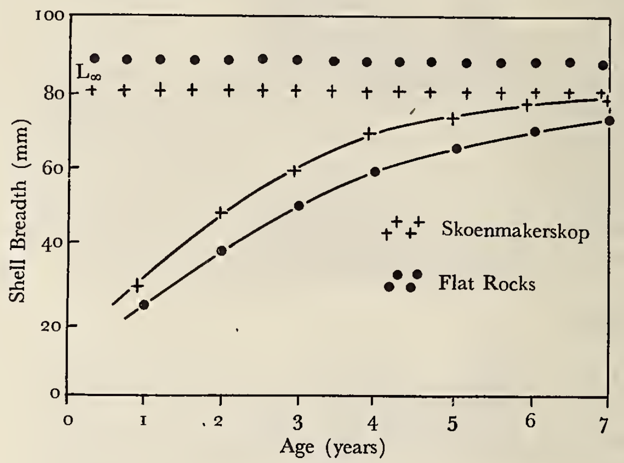


Figure 8

Ford-Walford plots for *Turbo sarmaticus* based on (1) tagging results from Skoenmakerskop; (2) population sampling results (histograms) from Skoenmakerskop; and (3) population sampling results from Flat Rocks

Production

Production estimates based on the population samples are given in Tables 1 and 2. Older year classes that could not be accurately separated were pooled. At Skoenmakerskop P_M exceeded P_G, indicating a drop in biomass over the study period. Steady state production ($\overline{P}$) was greatest for the older classes due to their large standing crops, but steady state production/biomass ratios ($\overline{P}/\overline{B}$) were maximum for the 0 + class. The low $\overline{P}/\overline{B}$ for the 1 + class is probably due to inaccurate separation of classes.

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Figure 7

Relationship between shell breadth and annual growth rate in *Turbo sarmaticus* based on tagging data and from size frequency histograms for Skoenmakerskop

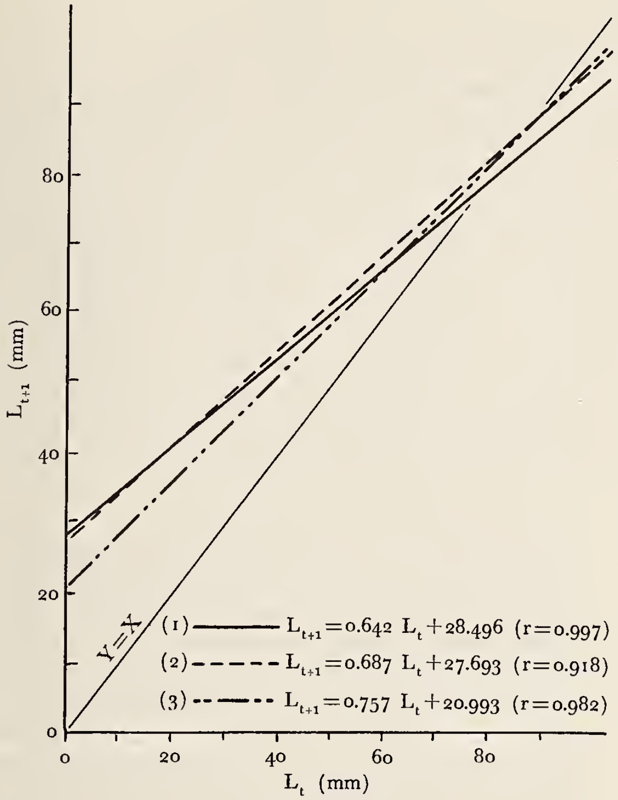

Figure 9

von Bertalanffy growth curves for *Turbo sarmaticus* from Skoenmakerskop and Flat Rocks

The overall mean biomass was $8.40 g.m^{-2}$ and the overall mean annual $\overline{P}/\overline{B}$ $0.48y^{-1}$.

At Flat Rocks the general pattern was similar but younger age classes made a greater contribution to total production. $\overline{P}/\overline{B}$ ratios decreased from younger to older age classes. The overall mean biomass and $\overline{P}/\overline{B}$ ratios were $1.71 g.m^{-2}$ and $0.69y^{-1}$. This area thus supports a smaller standing crop composed mainly of younger individuals. As a result of the higher $\overline{P}/\overline{B}$ ratios of younger classes, Flat Rocks thus has a higher overall $\overline{P}/\overline{B}$. Reproductive output ($P_R$) for these 2 populations has been estimated (LOMBARD, 1977) on the basis of changes in gonad mass in adults. This was found to give annual P_R/B ratios of $0.08y^{-1}$ and $0.07y^{-1}$ for Skoenmakerskop and Flat Rocks, making the $\overline{P}_{TOTAL}/\overline{B}$ ratios $0.56y^{-1}$ and $0.76y^{-1}$, respectively. The unexploited population at Skoenmakerskop thus exhibits higher biomass, greater contribution by adults, lower $\overline{P}_T/\overline{B}$ but slightly higher contribution to reproductive output than the exploited population at Flat Rocks.

The mean energy values of dry tissue of *Turbo sarmaticus* were $19.55 kJ.g^{-1}$ and $19.51 kJ.g^{-1}$ at Skoenmakerskop and Flat Rocks, respectively (MCLACHLAN & LOMBARD, 1979) and do not differ significantly (t-test). Production in energy terms thus amounted to $91.96 kJ.m^{-2}.^{-1}$ and $25.36 kJ.m^{-2}.y^{-1}$ at these 2 localities, respectively.

Because of widely differing numbers in different year classes no reliable estimate of mortality could be obtained for Skoenmakerskop. The rapid drop-off in num-

Table 1

Results of analysis of *Turbo sarmaticus* population at Schoenmakerskop over 460 days during 1975/6. $\overline{N}$ = mean numbers, $\overline{W}$ = mean mass, $\overline{B}$ = mean biomass, P_M = production by mortality, P_G = production by growth, $\overline{P}$ = steady state production.

	Year Class				
	0+	1+	2+	3+→	Total
$\overline{N}$ $460m^{-2}$	13.86	116.43	197.29	153.00	480.58
$\overline{W}$ g^{-1}	0.33	2.57	8.17	12.74	23.81
$\overline{B}$ g. $460m^{-2}$	4.58	299.51	1611.86	1949.22	3865.17
P_M g. $460m^{-2}460d^{-1}$	4.32	−313.14	750.80	2058.78	2500.76
P_G g. $460m^{-2}460d^{-1}$	13.42	424.67	1359.76	425.08	2222.93
$\overline{P}$ g. $460m^{-2}460d^{-1}$	8.87	55.77	1055.28	1241.93	2361.85
$\overline{P}/\overline{B}$ $460d^{-1}$	1.94	0.19	0.65	0.64	0.61
$\overline{P}/\overline{B}$ y^{-1}	1.54	0.15	0.52	0.51	0.48

Table 2

Results of analysis of *Turbo sarmaticus* population at Flat Rocks over 507 days during 1975/6. Symbols as in Table 1.

	Year Class					
	0+	1+	2+	3+	4+→	Total
$\bar{N}$ 600m^{-2}	322.29	116.71	105.57	38.43	17.14	600.14
$\bar{W}$ g^{-1}	0.22	1.30	3.04	7.43	11.58	23.57
$\bar{B}$ g. 600m^{-2}	70.90	151.72	320.93	285.53	198.48	1027.56
P_M g. 600m^{-2}507d^{-1}	251.54	285.40	403.04	316.95	54.65	1311.58
P_G g. 600m^{-2}. 507d^{-1}	199.45	−43.11	259.57	262.71	−11.60	667.02
$\bar{P}$ g. 600m^{-2}. 507d^{-1}	225.50	121.15	331.31	289.83	21.53	989.32
$\bar{P}/\bar{B}$ 507d^{-1}	3.18	0.80	1.03	1.02	0.11	0.96
$\bar{P}/\bar{B}$ y^{-1}	2.29	0.58	0.74	0.73	0.08	0.69

bers with age yielded a significant ($p < 0.05$) regression for Flat Rocks (Figure 10). From this the age specific mortality rate (Z) was calculated. $Z = 0.81^{-1}$, which gives an annual mortality rate ($1 - e^{-Z}$) of 0.56.

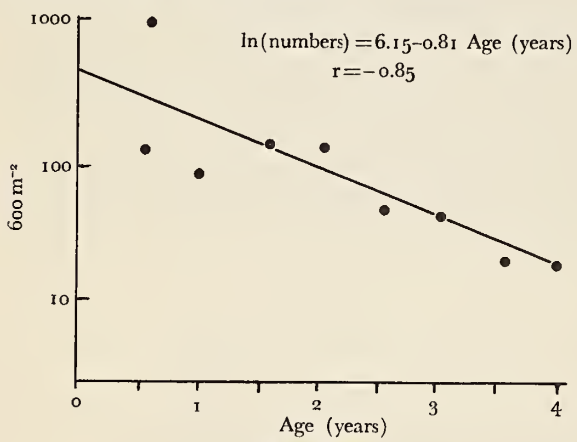

Figure 10

Survivorship/mortality of *Turbo sarmaticus* at Flat Rocks

DISCUSSION

Figure 2 indicates greater initial dry body mass per shell breadth at Skoenmakerskop than at Flat Rocks, but animals at the latter locality become heavier above a shell breadth of about 65 mm, although this difference is not statistically significant. The apparently greater dry mass of large (adult) individuals at Flat Rocks is probably due to greater gonad mass because animals for the breadth/mass regressions were collected in February which is the end of the ripe period at Flat Rocks, but 2 months after the ripe period at Skoenmakerskop (LOMBARD, 1977).

Seasonal growth was evident with maxima in summer for all size groups. NEWMAN (1968) found the reverse in *Haliotis midae* where the reproductive cycle influenced growth rates. BRANCH (1974) found slowest growth in winter when gonads develop in *Patella longicosta*. He also suggested that food value was an important determinant of growth in South African Patellidae. Seasonal changes in growth have also been ascribed to temperature (URSIN, 1965), food supply (COX, 1962) and reproductive cycle (SAKAI, 1962; BLACKMORE, 1969). As all 3 size classes of *Turbo sarmaticus* exhibited the same seasonal growth pattern, reproductive effects must be excluded and temperature or food, or both, are probably the major factors.

The 0+ class grew 23 mm at Flat Rocks and 29 mm at Skoenmakerskop in their first year. However, this difference is not significant (t-test). These values are based on the assumption that settlement occurred in July at both localities. It has already been stated that the ripe period at Flat Rocks is slightly later than at Skoenmakerskop and thus settlement may occur as much as one or two months later. Further, exploitation could be expected to cause a shift to the left of year class modes at Flat Rocks by removal of larger individuals. On the other hand, the slightly higher summer temperatures at Flat Rocks may accelerate growth there. Food is unlikely to be responsible for these differences as energy values of *Turbo sarmaticus* flesh from the 2 shores do not differ significantly.

The Flat Rocks population consisted mainly of 0-50 mm individuals and the removal of especially the larger animals is reflected in elimination (P_M) being nearly double production (P_G). The population was thus not in steady state during the study period. Settlement was extremely high, 1064 0+ animals being collected in the study area in February 1976. Numbers dropped rapidly, however, and there were less than 50 individuals older than 3 years. This is in marked contrast to Skoenmakerskop, where elimination and production nearly balanced and the population, dominated by adults, was in steady state. The maximum number of 0+ individuals collected at Skoenmakerskop was 44 (September, 1975), while more than 150 animals older than 3 years were present. There is thus a very stable adult population at Skoenmakerskop with low recruitment each year and the major mortality probably occurring before settlement. The low numbers of 0+ individuals during the study period (1+ animals were 4 times as abundant) may also be the result of a poor year and suggests fluctuations in recruitment.

Despite a much higher apparent settlement and a higher $\overline{P}/\overline{B}$ ratio, the exploited population at Flat Rocks had a biomass only 20% and mean annual production only 27% that at Skoenmakerskop. Converting production estimates over 1.5 years to annual values may involve some error as growth is seasonal and all seasons were not equally represented. However, the additional half year covered an equal proportion of warm and cold months so that seasonal growth differences should cancel out. The steady state $\overline{P}/\overline{B}$ ratios obtained are approximately as would be expected for a species with a maximum life span over 10 years and populations with the majority of individuals older than 1 year (WATERS, 1969; ZAIKA, 1972), but are low compared to values for some boreal molluscs (BURKE & MANN, 1974). Differences between these 2 populations may not only be due to exploitation as the effects of temperature and wave action have not been evaluated. However, the similarity of the growth and length/mass curves of the 2 populations suggests that these effects are small.

GOLIKOV & MENSHUTKIN (1973) state that quantitative relationships between supporting production, biomass and growth production may serve as a measure for assessing the degree of exploitation of a population. Supporting production (Ps) they define as the total biomass of individuals less than 1 year old plus the mass increase of older animals retained in the population. These values are as follows ($\overline{P}$ = steady state production):

	$\overline{P}$	Ps	$\overline{B}$	Ps/$\overline{B}$
Skoenmakerskop	$4.03 g.m^{-2}.y^{-2}$	$3.75 g.m^{-2}.y^{-1}$	$8.40 g.m^{-2}$	0.45
Flat Rocks	$1.17 g.m^{-2}.y^{-1}$	$0.98 g.m^{-2}.y^{-1}$	$1.71 g.m^{-2}$	0.57

The ratios $P_s/\overline{B}$ roughly fit the predictions of GOLIKOV & MENSHUTKIN (1973) on the basis of population age structure. P/P_s ratios are 1.07 for Skoenmakerskop and 1.19 for Flat Rocks.

The population structure at Flat Rocks suggests that exploitation starts well below the size of sexual maturity (about 60 mm shell breadth). Small animals are mostly collected for bait by anglers while the larger ones are eaten. The average meat (foot only) yield of a large specimen is about 8g dry mass. Bearing in mind the low biomass, relatively slow growth rate and this small yield, commercial exploitation of *Turbo sarmaticus* does not appear feasible unless very high prices could be obtained.

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